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Marcel G.A. van der Heijden[*1,2,3] & Cameron Wagg[1]

1. Ecological Farming Systems, Agroscope Reckenholz-Tänikon, Research Station ART, Reckenholzstrasse 191, CH-8046, Zürich, Switzerland.
2. Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurestrasse 190, CH-8057, Zürich, Switzerland.
3. Plant-Microbe Interactions, Institute of Environmental Biology, Faculty of Science, Utrecht University, 3508 TC, Utrecht, the Netherlands.

* Corresponding Author:

Email: marcel.vanderheijden@art.admin.ch

Feldfunktion geändert

Soil microbes represent the unseen majority of life on Earth and are essential for the functioning of terrestrial ecosystems as they catalyze unique and indispensable transformations in the biogeochemical cycles of the biosphere (Whitman et al. 1998, van der Heijden et al. 2008). The significance of soil microbial diversity for the functioning of agricultural and natural ecosystems is still poorly understood and soil microbial communities can be considered as a black box (Kennedy & Smith 1995; Cortois & de Deyn 2012). Unraveling what soil microbes are doing in this black box has been identified as one of the major research areas in science.

An increasing number of studies demonstrate that agricultural practices, such as tree based intercropping (Lacombe et al. 2009; Bainard et al. 2012), organic farming (Mäder et al. 2002; Bengtson et al. 2005; Birkhofer et al. 2008; Verbruggen et al. 2010), reduced soil tillage (van Capelle et al. 2012), crop rotation (Altierri et al. 1999; Cavagnaro et al. 2011) and land use extensification (Postma-Blaauw et al. 2010; de Vries et al. 2012) have a positive impact on the abundance and richness of specific groups of soil organisms (e.g. arbuscular mycorrhizal fungi, earthworms) and on soil microbial diversity. Thus, by adapting farm management practices it is possible to favor recruitment of specific groups of soil organisms and enhance microbial diversity. As such, these findings make it possible to provide policy makers with recommendation on enhancing soil biodiversity in agricultural ecosystems. There are a number of mechanisms by which microbial diversity can support agro-ecosystem functioning and particular ecosystem functions such as plant productivity and decomposition. For instance, microbes can form “consortia” that enhance plant productivity (e.g. when different microbes provide different limiting resources to plants) or decomposition (e.g. when plant material is decomposed by specialized microbes with unique physiological properties that succeed each other). As a consequence, microbial diversity can promote ecosystem

functioning. However, in other cases, the presence of keystone species (e.g. specific pathogens, nitrogen fixers) rather than diversity "*per se*" may determine agro-ecosystem functioning. Until now, it is still poorly understood whether increased soil (microbial) diversity is beneficial for the functioning and sustainability of agricultural systems.

In this issue (pp. xxx-xxx) an extensive study by Bainard and colleagues showed that things are certainly not simple. They used soil from conventional agricultural fields and from tree-based intercropping systems as inoculum in a glasshouse bioassay and assessed the influence of soil biotic communities conditioned by these two different practices on three agricultural crops. In earlier work it was shown that soils from tree based intercropping systems had higher microbial diversity compared to conventionally managed soils (Lacombe et al. 2009; Bainard et al. 2012b). Hence, it was hypothesized that plants would benefit when inoculated with soils derived from tree based intercropping systems. In contrast to their hypothesis, there were no differences in inocula effects between farming systems. Moreover, two of the three crops (barley and canola) grew best in soil with sterilized inoculum. Thus, the results from this study do not indicate that plants benefit from increased microbial diversity (but see below). Instead, soil pathogens appeared to be a stronger driver of plant productivity than diversity for two of the investigated crop species in this study.

Bottlenecks and advances

The great difficulty in assessing the impact of soil microbes on plant productivity and ecosystem processes arises since microbial diversity and abundance cannot be easily manipulated without simultaneously changing other factors or organisms (Read 2002).

69 Hence, it is a common approach to perform greenhouse experiments under controlled
70 conditions in sterilized soil and add soil inoculum (Bainard et al. 2012a, Verbruggen et al.
71 2012; Maheraldi & Klironomosi 2007 ; Wagg et al. 2011). By adding soil inoculum from fields
72 with different microbial diversity it is subsequently possible to mimic differences in microbial
73 communities under controlled conditions and test their impact on plants and ecosystems.
74 When doing this, it is important to verify that differences in soil microbial diversity are
75 responsible for observed effects. Consequently, it is required to demonstrate at the
76 beginning and at the end of the experiment that soil microbial diversity differs among
77 treatments. The experiments by Bainard et al. (2012a) were very large (750 pots) and hence
78 such information was not presented (e.g. it is extremely laborious and financially demanding
79 to determine microbial community composition of 750 pots). Thus, with the results
80 presented it was not possible to draw firm conclusions. Further work is needed to test
81 whether enhanced microbial diversity in tree-based intercropping systems can provide
82 additional ecological services to these systems.

83 A number of recent developments provide opportunities for understanding how soil
84 microbial communities influence the productivity and sustainability of cropping systems.
85 First, costs for the molecular characterization of microbial communities (e.g. by high
86 throughput sequencing) has declined considerably in recent years, making it now possible to
87 characterize microbial communities for a larger number of samples. Second, fluxes of
88 carbon and nutrients that are mediated by microbes can be measured with (stable) isotopes
89 and related technology such as stable isotope probing (e.g. Vandenkoornhuyse et al. 2007;
90 Kiers et al. 2011). With these techniques it is possible to show which microbes are active,
91 thus providing mechanistic insights into the role of specific soil microbial communities in
92 driving ecosystem functioning. Third, it is difficult to manipulate microbial diversity because

93 many microbes readily disperse via air and water. As a consequence, microbes can easily
94 contaminate pots and cause unwanted changes in experimental treatments. Hence,
95 differences in the effects of microbial diversity at the start of the experiment may eventually
96 disappear, especially if experiments are performed over longer periods of time. Recently, we
97 developed an experimental system in which it is possible to manipulate microbial diversity in
98 experimental ecosystems without contamination from the outside (Figure 1). Such tools
99 provide new avenues for testing whether soil microbial diversity influence ecosystem
100 functioning and whether soils with high microbial diversity are important for sustaining
101 agricultural production.

102

103 ***Applicability of soil biodiversity research in Agro-Ecosystems***

104 The experiments by Bainard et al. also show that growth responses of crops in response to
105 soil inoculation are variable. Barley and canola performed best in sterilized soil and these
106 crops also did not benefit from the presence of arbuscular mycorrhizal (AM) fungi, soil fungi
107 that facilitate plant growth by providing plant inaccessible nutrients. This is perhaps to be
108 expected since canola does not form AM fungal associations and a number of studies
109 showed that barley does not necessarily benefit from AM fungi (e.g. Grace et al. 2009). Thus,
110 it appears that the impact of plant antagonists of these crops on productivity was larger than
111 those of beneficial soil organisms. In contrast, soybean grew equally well in sterilized and
112 non-sterilized soil and in a second experiment, Bainard et al. demonstrate soybean
113 performed better in pots inoculated with AM fungi, which is typical of most legumes. Thus,
114 the effects of soil organisms on crops is driven by the species identity and plant functional
115 group of the crop, making it difficult to make general recommendations about the benefits

of soil microbial diversity in agro-ecosystems. Moreover, microbes not only influence plant productivity, but a wide range of ecosystem functions are affected by soil microbes that indirectly affect plant productivity, not only within a growing season but also over time. (nutrient losses, nutrient cycling, soil structure stabilization etc. – see van der Heijden et al. 2008). Such indirect effects should not be overlooked when assessing the importance of soil microbial diversity.

In conclusion, there are now a wide range of studies describing how soil organisms and soil microbes respond to different agricultural practices. However, current understanding as to whether such changes in soil (microbial) diversity are beneficial for the functioning of agro-ecosystems is only in its infancy. Only a few studies, often theoretical or performed under highly controlled conditions with a particular group of micro-organisms indicate that enhanced microbial diversity can indeed be beneficial by providing a number of ecosystem services (Brussaard et al. 2007; van der Heijden et al. 2008; Berendsen et al. 2012). The work by Bainard et al. provide new insights into the role of soil microbes in agro-ecosystem demonstrating negative soil feedback to be a strong mechanism. At the same time these authors also illustrate there remain many important questions to be addressed about the role of soil biodiversity in agro-ecosystems and its applicability.

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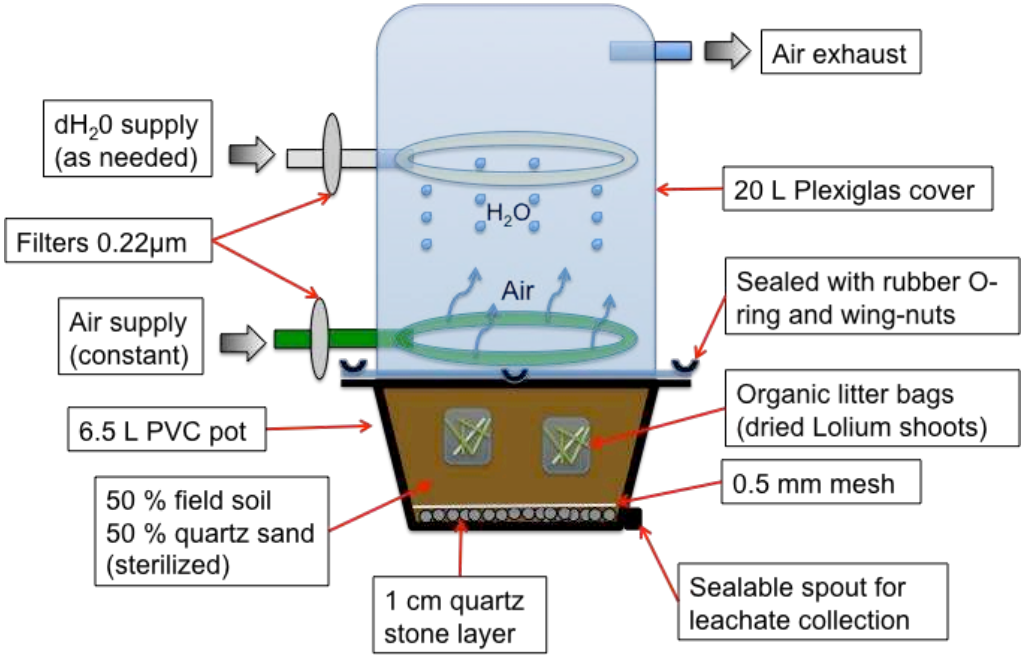
Air exhaust
dH20 supply (as needed)
20 L Plexiglas cover
H2O
Filters 0.22µm
Air
Sealed with rubber O-ring and wing-nuts
Air supply (constant)
Organic litter bags (dried Lolium shoots)
6.5 L PVC pot
0.5 mm mesh
50 % field soil
50 % quartz sand
(sterilized)
Sealable spout for leachate collection
1 cm quartz stone layer

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Figure 1: *Schematic draw (a) and photograph (b) of an experimental microcosm in which plants can be grown under controlled conditions without microbial contamination from the outside. In order to prevent microbial contamination, filling and planting of the microcosms*

needs to be performed in a laminar flow hood and all material needs to be sterilized or autoclaved before use. Moreover, during the growth period, incoming pressured air is filtered through a hydrophobic filter (0.22 µm), while water/nutrient solution is filtered through a hydrophilic filter (0.22 µm) to prevent contamination from the outside. Replicated microcosms can be inoculated with soil inoculum from different agricultural fields or microcosms can be inoculated with different (numbers of) microbes. Litter bags or hyphal compartments with labelled material (^{13}C and or ^{15}N) can be added to the microcosms in order to test whether decomposition and/or nutrient uptake varies between microcosms with different microbial diversity treatments. $^{13}CO2$ can be added to the microcosms (instead of pressured air) to trace the fate of assimilated C (to facilitate stable isotope probing). Microcosm Design: Marcel van der Heijden & Susanne de Bruin.